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Research article

# Phenotypic correlates of potential range size and range filling in European trees

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ABSTRACT

Understanding the biological correlates of range sizes in plant species is important to predict the response of species to climate change. We used climate envelope models to estimate species' potential range size and range filling for 48 European tree species. We hypothesized that potential range size relates to the climatic tolerances of plant species, and that the degree of range filling is influenced by species dispersal. We tested these hypotheses using, for each species, estimates for tolerance to cold and drought, type of dispersal, fruit size and seed size. Consistent with previous observations, we found that both the size of potential ranges and range filling increase from south to north. Species tolerance to temperature and water stress, as well as their dispersal-related traits also showed marked spatial patterns. There was, moreover, a significant positive partial correlation between cold tolerance and potential range size, when drought tolerance was partialed out, and a non-significant partial correlation between drought tolerance and potential range size, with cold tolerance partialed out. Range filling was not significantly larger in species dispersed by wind than in those dispersed by animals. There was a negative correlation between seed mass and range filling, but its statistical significance varied across different subsets of species and climate envelope algorithms; the correlation between fruit length and range filling was not significant. We conclude that climatic tolerances and dispersal traits influence species range size and range filling, and thus affect the range dynamics of species in response to global change. Using traits will therefore help to predict future distribution of species under climate change.


## Introduction

The idea that climate limits the distributions of plants was formalized through the 'law of tolerance' formulated by Shelford (1913). The hypothesis states that the tolerance of plant species to both deficiency and excess of factors that affect organisms determines the range of values along an environmental axis in which it can survive, that is the tolerance range. More recent theoretical studies propose that birth and death rates are, at least in part, controlled by the interplay between the abiotic variables

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and the tolerances of species to these variables (Osmond et al., 1987), with populations declining as conditions depart from the species-specific optima (Hengeveld and Haeck, 1982). It follows from this reasoning that a positive relationship between the climatic tolerances of species and their range sizes should exist, since greater tolerances would necessarily imply that greater amounts of environmental suitability would be available for species (Williams et al., 2007). Also, range size might be controlled by the dispersal ability of species (Baselga et al., 2012). The 'site colonization hypothesis' (Lester et al., 2007) is likely to operate when species had relatively little time to expand their ranges from glacial refugia (Svenning et al., 2008). In this case, a relationship between dispersal-related traits and the occupied fraction of the potential range ('range filling') would be expected. Range size may also be time-limited over macroevolutionary scales, increasing with species age (Paul et al., 2009) as originally proposed by Willis (1922) in his 'age-and-area hypothesis', although the predictions arising from this hypothesis have not been confirmed in a number of studies (e.g. Jablonski, 1987). In conclusion, the size of geographical ranges should at least partly be explained by species-specific tolerances and dispersal capacities.

Many studies have correlated the range of species with extrinsic factors such as climate, topography or distances to Pleistocene refugia (Svenning and Skov, 2004; Angert et al., 2011), but very few have integrated at large scales the role of phenotypic traits and other intrinsic factors to understand why some species inhabit and colonize different regions. Here, we focus on phenotypic correlates of potential range size and range filling as provided by climate envelope models (CEMs). We analyze trait-based drivers of variation in range size using information about the distribution of 48 European tree species, their species-specific tolerances to climate, and their dispersal capacities, while taking into account potential phylogenetic effects on range heritability (Diniz-Filho et al., 2012a,b). We only use climatic variables to model the potential distribution of species for making our findings most relevant to understand the future distribution of species under climate change.

Specifically, we determine the spatial patterns (1) in potential range size, and range filling of European tree species; (2) of tree species tolerance to cold and drought; and (3) of traits related to species dispersal such as vector of dispersal, fruit size and seed size. We hypothesize also that the potential range sizes of species are related to their climatic tolerances, i.e. tolerance to cold and drought. We specifically test (4) whether the potential range size of tree species correlates with cold and drought tolerance. Finally, we investigate (5) whether range filling is affected by the type of dispersal and diaspore (fruit or seed) size. We hypothesize that range filling will increase with increasing dispersal ability. Therefore, range filling should increase with decreasing seed size, because small-seeded species tend to be dispersed by wind over greater distances than large-seeded, zoochorous tree species (Guo et al., 2000; Morin and Chuine, 2006; Cousens et al., 2008). All analyses were carried out after accounting for phylogenetic signals.

**Table 1**
List of study species, their potential and realized range size, and range filling. Nomenclature follows Atlas Flora Europaeae.

| Species | Potential range (Mio km$^2$) | Realized range (Mio km$^2$) | Range filling (%) |
|---|---|---|---|
| *Abies alba* | 3.1 | 1.1 | 34.7 |
| *Abies cephalonica* | 0.5 | 0.1 | 10.7 |
| *Alnus cordata* | 0.1 | 0.0 | 35.0 |
| *Alnus glutinosa* | 3.8 | 4.0 | 104.2 |
| *Alnus incana* | 3.1 | 2.6 | 85.5 |
| *Betula pendula* | 3.4 | 3.6 | 106.7 |
| *Betula pubescens* | 3.3 | 3.3 | 99.1 |
| *Carpinus betulus* | 2.8 | 2.4 | 83.0 |
| *Castanea sativa* | 3.2 | 0.6 | 18.9 |
| *Celtis australis* | 3.2 | 0.6 | 19.0 |
| *Corylus colurna* | 1.8 | 0.2 | 11.9 |
| *Cupressus sempervirens* | 1.2 | 0.0 | 2.5 |
| *Fagus orientalis* | 0.3 | 0.1 | 28.3 |
| *Fagus sylvatica* | 3.0 | 2.6 | 85.4 |
| *Juglans regia* | 2.1 | 0.3 | 13.4 |
| *Juniperus excelsa* | 0.6 | 0.0 | 8.6 |
| *Juniperus thurifera* | 2.6 | 0.1 | 4.8 |
| *Larix decidua* | 1.9 | 0.4 | 20.4 |
| *Laurus nobilis* | 1.3 | 0.4 | 27.5 |
| *Ostrya carpinifolia* | 2.9 | 0.6 | 20.9 |
| *Picea abies* | 2.4 | 2.1 | 87.3 |
| *Pinus brutia* | 0.4 | 0.0 | 5.9 |
| *Pinus cembra* | 1.7 | 0.2 | 10.7 |
| *Pinus halepensis* | 1.3 | 0.3 | 26.2 |
| *Pinus heldreichii* | 1.7 | 0.1 | 4.8 |
| *Pinus mugo* | 2.6 | 0.5 | 21.1 |
| *Pinus nigra* | 2.8 | 0.5 | 17.0 |
| *Pinus peuce* | 0.8 | 0.1 | 8.0 |
| *Pinus pinaster* | 1.2 | 0.4 | 29.8 |
| *Pinus pinea* | 0.9 | 0.2 | 27.3 |
| *Pinus sylvestris* | 3.6 | 2.8 | 78.3 |
| *Platanus orientalis* | 1.3 | 0.2 | 16.5 |
| *Populus alba* | 3.3 | 1.7 | 51.9 |
| *Populus nigra* | 3.1 | 2.2 | 72.3 |
| *Populus tremula* | 3.9 | 4.1 | 105.7 |
| *Quercus cerris* | 2.5 | 0.9 | 36.1 |
| *Quercus faginea* | 1.3 | 0.4 | 28.7 |
| *Quercus frainetto* | 2.1 | 0.5 | 26.0 |
| *Quercus ilex* | 1.9 | 1.0 | 54.7 |
| *Quercus petraea* | 3.0 | 2.9 | 96.2 |
| *Quercus pubescens* | 2.9 | 0.5 | 15.8 |
| *Quercus pyrenaica* | 1.1 | 1.6 | 140.5 |
| *Quercus suber* | 1.0 | 0.4 | 41.7 |
| *Salix alba* | 3.5 | 3.0 | 85.9 |
| *Salix caprea* | 3.8 | 4.0 | 104.6 |
| *Salix fragilis* | 3.3 | 2.5 | 74.9 |
| *Taxus baccata* | 3.4 | 1.6 | 47.3 |
| *Ulmus glabra* | 3.3 | 2.8 | 85.4 |
| *Ulmus laevis* | 2.4 | 1.3 | 56.0 |

## Material and methods

### *Source data on species distribution and climatic conditions*

The study area encompasses Europe between latitudes 34–72° N and longitudes 11° W to 32° E. Species records east of this geographical window were excluded, because of uneven quality of the original species distributions data in these areas (Williams et al., 2000). Within this constrained geographical window, we measured range size of all major European tree species for which trait data, and consistently mapped distributions, were available. We defined trees as self-supporting woody species reaching ≥20 m in height, or species falling just under this limit (More and White, 2003). Species selection was constrained by data availability on geographical distribution, climatic tolerances and dispersal capacities. The final list contained 48 tree species with complete information (Table 1). Nomenclature and information about the distributions of the selected species were taken from Atlas Flora Europaea, AFE (Jalas and Suominen, 1972–1996; www.fmnh.helsinki.fi/english/botany/afe). The records in AFE were mostly from native origin, though populations with unknown status were also considered if they had been present for a long time. We restricted modeling to species occurring in at least ten AFE cells to avoid problems of fitting models with extremely small sample sizes (Stockwell and Peterson, 2002; Munguía et al., 2012). The AFE used near-equal area mapping units of 50 km × 50 km (Williams et al., 2000; Nogués-Bravo and Araújo, 2006), based on the Universal Transverse Mercator projection and the Military Grid Reference System, hereafter referred to as AFE cells.